



A new butterfly species from the Colombian Andes and a review of the taxonomy of the genera *Idioneurula* Strand, 1932 and *Tamania* Pyrcz, 1995 (Lepidoptera: Nymphalidae: Satyrinae)

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Abstract

A new species of the genus *Idioneurula* Strand, 1932 is described from high elevation habitats (páramos) of the Serranía de los Yariguíes, Santander Department, in the eastern Andes of Colombia. Aspects of the ecology, distribution and conservation of the new species are presented. The taxonomy of this genus and closely related *Tamania* Pyrcz, 1995 are discussed. Based on adult morphology and supported by preliminary molecular analysis, it is proposed that the name *Tamania* Pyrcz, 1995 be treated as a junior subjective synonym of *Idioneurula* Strand, 1932. We propose treating *Idioneurula* as comprising four species: *I. erebioides* (C. Felder & R. Felder, 1867); *I. donegani* Huertas & Arias, **n. sp.**; *I. eremita* Vilorio & Pyrcz, 2007; and *I. jacquelinae* (Pyrcz, 1995). *I. erebioides* f. *moderata* (Weymer, 1911) and *I. erebioides* f. *intermedia* (Apolinar, 1914) are not recognised as valid taxa.

Key words: Colombia, Serranía de los Yariguíes, *Idioneurula donegani* **n. sp.**, *Idioneurula erebioides*, *Idioneurula eremita*, *Tamania jacquelinae*, conservation

Resumen

Se describe una nueva especie del género *Idioneurula* Strand, 1932 colectada en los páramos de la Serranía de los Yariguíes, Santander, cordillera oriental de Colombia. Se presentan aspectos de la ecología, distribución y conservación de la nueva especie. La taxonomía de *Idioneurula* Strand, 1932 y el género relacionado *Tamania* Pyrcz, 1995 es discutida. Basado en la morfología del adulto y apoyado con un análisis molecular preliminar se propone que el género *Tamania* Pyrcz, 1995 sea tratado como sinónimo subjetivo de *Idioneurula* Strand, 1932. También se propone que el género *Idioneurula* en adelante, comprenda cuatro especies: *I. erebioides* (C. Felder & R. Felder, 1867); *I. donegani* Huertas & Arias, **n. sp.**; *I. eremita* Vilorio & Pyrcz, 2007 y *I. jacquelinae* (Pyrcz, 1995). *I. erebioides* f. *moderata* (Weymer, 1911) e *I. erebioides* f. *intermedia* (Apolinar, 1914) no se reconocen como taxones válidos.

Palabras clave: Colombia, Serranía de los Yariguíes, *Idioneurula donegani* **n. sp.**, *Idioneurula erebioides*, *Idioneurula eremita*, *Tamania jacquelinae*, conservación

Introduction

The Satyrine butterflies (Lepidoptera: Nymphalidae: Satyrinae) are cosmopolitan (Ackery *et al.* 1999) but are not yet well studied in the tropical Andean region, due to their taxonomic complexity, morphological homogeneity and frequent restriction to remote, high elevation regions (Pyrcz & Wojtusik 1999; Vilorio 2003; Huer-

tas 2004; Peña & Lamas 2005; Wahlberg *et al.* 2005; Pyrcz & Vilorio 2007). Nonetheless, the Satyrinae have recently become a focus of research attention as a proposed ecological indicator group (Adams & Bernard 1979; Vilorio 1998, 1999; Pyrcz & Wojtusiak 1999; Pyrcz 1995; Huertas 2004) and the subject of molecular phylogenetic studies (Peña *et al.* 2006). These studies and others have led progressively to an increase in our knowledge of the taxonomy, biology and phylogenetic relationships of the group and more recently, the description of several new taxa (e.g. Pyrcz 1995; Willmott & Hall 1995; Pyrcz & Vilorio 1999; Pyrcz *et al.* 1999; Vilorio & Pyrcz 2000; Pyrcz 2004; Peña & Lamas 2005; Freitas & Peña 2006; Pyrcz 2006; Pyrcz *et al.* 2006).

The Satyrinae includes the high elevation north Andean genus *Idioneurula* Strand, 1932 (formerly *Idioneura* C. Felder & R. Felder, 1867: a preoccupied name). Until very recently, *Idioneurula* had been regarded as containing only one species, *Idioneurula erebioides* (C. Felder & R. Felder, 1867). The genus has been placed in the tribe Satyrini, either in the subtribe Erebiina (Lamas & Vilorio 2004; Vilorio 2007) or Pronophilina (Peña *et al.* 2006). *Idioneurula erebioides* has been reported from Colombia (Cundinamarca and Boyacá departments) and uncertainly from Venezuela (a specimen so labelled at BMNH). Two specimens of *I. erebioides* in the Natural History Museum London (BMNH) from “Bolivia” are probably mislabelled, as are two specimens of *T. jacquelinae* also labelled “Bolivia” (Pyrcz 1995). Two forms of *Idioneurula erebioides* have been described as *f. moderata* (Weymer, 1911) and *f. intermedia* (Apolinar, 1914). These names were synonymised by Lamas & Vilorio (2004) with nominate *I. erebioides*. A new species of *Idioneurula* was recently described from the Colombia-Venezuela border: *I. eremita* Vilorio & Pyrcz, 2007. Taxonomy used herein generally follows Lamas & Vilorio (2004).

The monobasic and closely related genus *Tamania* Pyrcz, 1995 has been placed as sister to *Idioneurula* in recent studies (Lamas & Vilorio 2004; Peña *et al.* 2006; Pyrcz & Vilorio 2007), although *I. erebioides*, the type species of *Idioneurula*, has not been sampled in published molecular studies. *Tamania jacquelinae* Pyrcz, 1995 is considered endemic to the Tamá massif on the Colombia-Venezuela border (Pyrcz 1995). All known species of *Idioneurula* and *Tamania* are rather similar in appearance. They are small-medium sized, plain brown butterflies with a variable number of ocelli on their hind wings. Patterns on the ventral hind wings vary considerably intraspecifically in some species (see discussion below). *Idioneurula* species are found mainly in high elevation habitats (páramos) of Colombia and Venezuela, but their complete range is not known due to a lack of collecting initiatives in high elevations in the region (which itself is partially due to historical security concerns). It is possible that other species in the genus could remain undiscovered. Host plants also remain unknown for some species, although Poaceae is the usual host plant of many Satyrinae (DeVries 1987; Ackery 1988; Robinson *et al.* 2002) and a Cyperaceae is the host plant for *T. jacquelinae* (Pyrcz & Vilorio 2007).

The purpose of this paper is to describe a new species of *Idioneurula* found recently by the authors in Serranía de los Yariguíes, Colombia and to compare it to its apparent relatives. We further examine the taxonomy and distribution of other described taxa in the genera *Idioneurula* and *Tamania*.

Locality and methods

Serranía de los Yariguíes (previously known as Serranía de los Cobardes) is an isolated northwest spur between 6°N and 7°N located in Santander Department, on the western slope of the Cordillera Oriental of Colombia (Fig. 1). It reaches approximately 3400 m above sea level and has been unstudied for decades due to political instability. Between 2003–2006, the fauna of Serranía de los Yariguíes was studied for the first time by researchers on the Colombian EBA Project (Evaluation of Biodiversity in the Andes) and later the YARÉ Project (Yariguíes Assessment and Research of Endangered species) (Donegan *et al.* 2003; Huertas 2004; Donegan & Huertas 2005; Huertas & Donegan 2006). Pristine forest covers most of the western slope and ridgeline of Serranía de los Yariguíes, whilst the eastern slope is largely deforested. Surveys were con-

ducted in different habitats on the western slope ranging from 100 to 3000 m (the highest elevation site being accessed by helicopter) and on the eastern slope from 2000 to 3200 m (see details in Donegan & Huertas 2005; Huertas & Donegan 2006). Two of these sites were located in páramo habitat at the highest elevations. Following standard protocols (described further in Huertas 2004; Huertas & Arias 2005; Huertas & Ríos 2006), 28 individuals of an apparent *Idioneurula* species were collected.



FIGURE 1. Map of northern Colombia and western Venezuela showing localities where *I. donegani* Huertas & Arias, n. sp. was found (Serranía de los Yariquies: red dots). Other symbols show collecting localities of *I. erebioides* (Santander, Boyacá: blue squares), *I. eremita* (Tamá: pink triangles) and *T. jacquelinae* (Tamá: black dot). **A.** Digital elevation map in bottom right shows isolation of Serranía de los Yariquies highlands from the rest of the Cordillera Oriental.

Morphological characters and patterns were examined in all specimens collected and from other *Idioneurula* species deposited in the following visited collections:

BMNH	Natural History Museum, London, UK.
EHPC	Efraín Henao Personal Collection Manizales, Colombia.
IAvH	Instituto Alexander von Humboldt, Villa de Leyva, Colombia
JFLCPC	Jean François Le Crom Personal Collection, Bogotá, Colombia.
MCPC	Mauro & Clara Costa Personal Collection, Caracas, Venezuela.
MIZA	Museo del Instituto de Zoología Agrícola, Maracay, Venezuela.
MNHN	Museum National d'Histoire Naturelle, Paris, France.
MHN-US	Museo de Historia Natural, Universidad de la Salle, Bogotá, Colombia.
MHN-UC	Museo de Historia Natural, Universidad de Caldas, Manizales, Colombia.
NHM-OU	Natural History Museum, Oxford University, UK.

Dissections of genitalia were made of individuals of both sexes in available species (*I. donegani* and *I. erebioides* both male and female; and *I. eremita* and *T. jacquelinae* males only) following standard techniques. Photographs of genitalia were taken using Nikon Coolpix 4500 camera and compared with diagrams in Vilorio (1998), Pyrcz (1995) and Pyrcz & Vilorio (2007). Genitalia terminology herein follows Klots (1970). Dig-

ital photographs of adult live and mounted specimens were taken using Olympus Camedia C70 4.0mpx and Nikon Coolpix 8700 8.0mpx cameras respectively.

One individual of *I. donegani* was sequenced for mtDNA (*cox-1*) and compared with published mtDNA data for *I. eremita* and *T. jacquelinae* (Peña *et al.* 2006). PCR analysis was conducted using two primers using standard *cox-1* annealing conditions (47°C annealing temperature) from a single leg from the dried specimen and then sequenced using *ubc9* (Huertas & Lees unpub. data). Sequencher 4.5 (GeneCodes Corporation) and BioEdit V. 7.0 (Hall 1997–2005) were used for editing and alignment respectively. Pairwise comparisons with possible relatives were calculated and a preliminary tree including *I. eremita*, *T. jacquelinae* and *I. donegani* was produced.

Systematics

Idioneurula donegani Huertas & Arias, new species

Holotype m: Colombia, Santander, Serranía de los Yariguíes, Municipios El Carmen/Simacota, Lepipuerto 3000m, 06°28'N; 73°28'W, west slope; January 2005 (Huertas & Arias *leg.*). Deposited in IAvH, Colombia.

Allotype Colombia, Santander, Serranía de los Yariguíes, Municipio de Galán, Filo Pamplona 3200m, 06°38'N; 73°24'W; east slope. June–July 2005 (Huertas, Arias & Ríos *leg.*) **Paratypes** 7m, same data as the holotype. 14m and 2f, data as the allotype. Deposited in MHN-UC, JFLCPC and to be deposited in BMNH and other collections. No other specimens of *I. donegani* were found in the consulted collections or at other study sites in the Yariguíes.

For specimens of other taxa consulted in collections, see **Appendix I**.

Diagnosis. *Idioneurula donegani* **n. sp.** most closely resembles the two described *Idioneurula* species (*I. erebioides* and *I. eremita*) and *Tamania jacquelinae* in its morphology (Figs. 2A–D). *Idioneurula* are small to medium sized butterflies with a rather triangular-shaped forewing, plain brown coloured wings, no markings on the dorsal forewing, at least one ocellus on the lower border of the dorsal hindwing, such ocelli generally black with a yellow or orange border and white centre spot, no marked sexual dimorphism, high elevation distribution in the East Andes (Fig. 1), broadly similar male genitalia with proximal opening for the aedeagus hirsute and concave and small spines on the proximal tip of the aedeagus (Figs. 3A–D).

I. donegani **n. sp.** differs from *I. erebioides* and *I. eremita* in its larger overall size (wings: Table 1, antennae and abdomen), dark antennae (with no yellowish tip), wing shape (more rounded in *I. donegani*, more triangular in *I. erebioides* and *I. eremita*), absence of scales on borders of wing forming a hairy appearance, darker dorsal coloration of both wings, greater number of ocelli (always 4 or 5) on dorsal hind wing (HW) (from *I. erebioides* only) and ventral HW underside pattern; presence of dark brown zigzagging postmedian line and a series of 4–5 small submarginal ocelli with white pupils, similar to *I. eremita*, whereas in *I. erebioides* the pattern is indistinct, the ocelli faint or absent and the ventral HW often has intervenous cream stripes; and in male genitalia by a process of heavily sclerotization on dorso-distal valva. *Idioneurula donegani* differs from *T. jacquelinae* in its wing ground colour being less chestnut-brown in males and in the presence of zigzag pattern on HW; absence of ocelli on dorsal forewing (FW) (Figs. 2A–D); and in male genitalia as for the other species above. Notably, Pyrcz (1995) gave as diagnostic feature of *Tamania* that it exhibited “only one prominent M2–M3 cell ocellus on the upper and under surface of both wings”. *Idioneurula donegani* lacks this ocellus on the FW (Fig. 2). Despite the general similarity in size, differences are observed in average wing length between these species (Table 1). *I. donegani* has a greater range of variation in this measurement perhaps due to sampling in two different and distant localities.

Morphology. MALE: (Fig. 2A, Figs. 5C–F). **Head:** Eyes naked, dark coffee brown; palpi three times longer than head, densely hirsute, dorsally light brown, ventrally brown; antennae composed of 34 segments,

brown except for dorsal surface of club, which is light orange chestnut, shaft with brown scales on dorsal and white on ventral sides, club 2.5 times as broad as shaft. **Thorax:** dark brown, covered with hairy scales. **Abdomen:** dorsally dark brown. Ventrally gray with many scales. **Wings** (Fig. 4): Forewing mean 23.7 mm; range 20.6–27.5 (n=22), hairy, dorsally lustrous reddish brown (average 10YR 2/2 in Munsell (1977, 2000); cf. average 7.5YR 3/4–4/6 in *I. erebioides*), ventrally lighter and more brilliant. FW roughly triangular, apex and tornus obtuse; Sc independent of R1–R2. FW ground colour brown, progressively darker towards base, ventral discal region limited by two zigzag dark brown lines and another similar orange line separating marginal and submarginal regions and ventral FW wing edges, flanked with orange scales. Sparse reddish scales over all FW and HW. HW oval, margins rounded. Dorsal ground colour dark brown with thinly mottled orange scales around medial region; dark and tiny brown scales flanking margins of wings; two strongly marked dark brown zigzag lines, bordered with a thin line of orange scales, limiting submarginal area; dark brown line in marginal region bordering wing; between the lines are a series of four ocelli in cells M2-M3 to Cu1-Cu2, first three 3–4 mm diameter, whilst a fifth ocellus in Cu2-1A is reduced to 2–3 mm or less, sometimes vestigial but never absent; ocelli black, circled by ochreous yellow and finely pupilled with white. HW ventral ground colour brown (lighter than dorsal) darker towards base with two thin dark brown zigzag lines limiting submarginal region; ventral surface densely covered with short hair scales; series of four or five small ocelli from cell M2-M3 to Cu2-A1, black, pupilled with white and diffusely circled by yellow ochreous and dusted with reddish scales. **Genitalia:** (Figs. 3A–D). Uncus elongated, ending with a rounded hook. Subuncus short, about one third length of uncus, horn-shaped and slightly pointed. Valva medium-sized, wide dorsal process of valva, rounded tegument and heavily sclerotized disto-dorsally. Vinculum rather long and thin. Aedeagus thin and long with small spines on the proximal tip and proximal opening concave and hirsute. Immature stages unknown.

TABLE 1. Comparison between measures of forewing length taken in all known *Idioneurula* species and *Tamania jacquelinae*. m: male and f: female. *I. eremita* (data from Pyrcz & Vilorio 2007).

Species	FW length: m: male; f: female; mean (mm); minimum-maximum (mm); (n= sample size)
<i>I. erebioides</i>	All: 18.3; 16.0–21.1; (n=53) m: 18.4; 16.0–21.0; (n=40) f: 18.2; 16.5–21.1; (n=13)
<i>I. eremita</i>	All: 18.5; 17.0–21.0; (n=104) m: 19.0; 18.5–21.0; (n=80) f: 18.09 ; 17.0–20.0; (n=24)
<i>I. donegani</i>	All: 23.8; 21.0–27.5; (n=25) m: 23.7; 21.0–27.5; (n=22) f: 24.7; 24.0–26.0; (n=3)
<i>T. jacquelinae</i>	All: 21.4; 20.5–22.0; (n=7) m: 21.5; 20.5–22.0; (n=6) f: 21.0; (n=1)

FEMALE: Forewing mean 24.7mm; range 24.0–26.0 (n=3). Similar to male except as follows. Forewing length slightly longer on average. Wing shape more rounded on average. Background pattern similar to males but zigzag more strongly marked in dorsal forewing. Colour c. 3/3 10YR (Munsell 1997, 2000), as *T. jacquelinae*, paler than males on average. Line in hindwing marginal border more yellow (intense). Ocelli larger and five present on all specimens. Three to four ocelli in ventral hindwing. **Genitalia:** (Figs. 3E–F) Large sclerotized sterigma broadly rounded, with conspicuous “nose” beneath ostium bursae. Ductus bursae very short; corpus bursae large, membranous almost spherical, paired signum composed of two narrow bands of densely set teeth, signa almost as long as corpus bursae.

Distribution. *Idioneurula donegani* is known only from Serranía de los Yariguíes, in páramo habitat at 2900–3200m elevation. *Idioneurula erebioides* is found at similar elevations (2250–3200m) but in the main East Andes and ranges further south (Cundinamarca to Boyacá: found at Arcabuco, SFF Iguaque, Sierra Nevada del Cocuy and Bogotá region). *I. erebioides* and *I. donegani* are not known to be sympatric (**Fig. 1**). On the north-eastern slope of the Cordillera Oriental in the region of Tamá, *Tamania jacquelineae* (2200–2500m) and *Idioneurula eremita* (2400–3350m) are found, with the latter replacing the former at higher elevations (Pyrce 1995; Vilorio 1998). *Idioneurula donegani* has not been found in the main range of the East Andes, suggesting that it may be endemic to Serranía de los Yariguíes. The páramo habitats of the Yariguíes are isolated from others in the northern East Andes by a dry region of lower elevation in the valleys of the rivers Chicamocha and Suárez and by depressions associated with the ríos Horta and Opón. The isolation of the Yariguíes páramo systems possibly may have led to differentiation of high elevation taxa such as *I. donegani*. Several endemic undescribed bird taxa were also found in the Yariguíes páramo (Donegan *et al.* 2007).

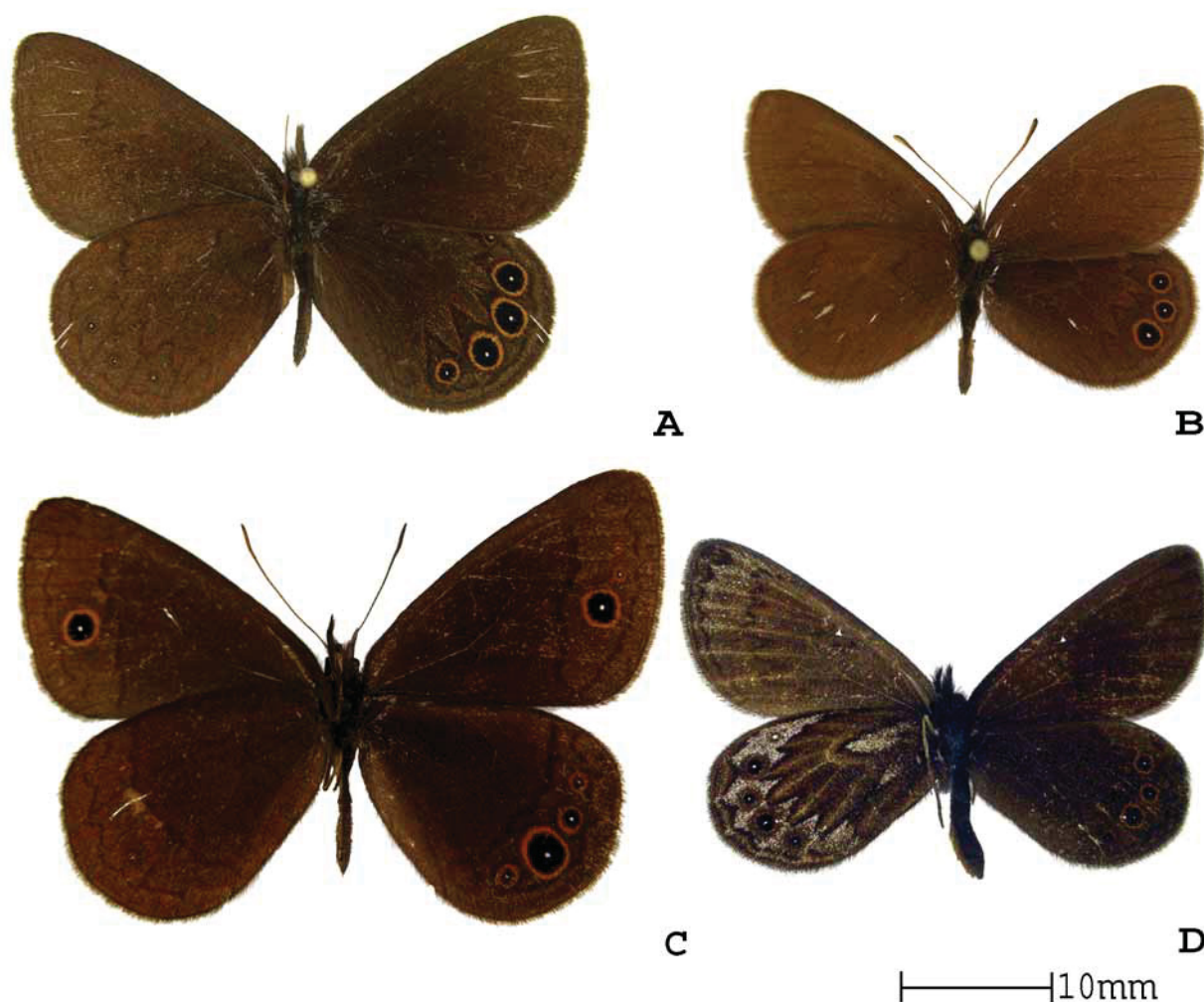


FIGURE 2. *Idioneurula* and *Tamania* adult male species. **A.** *I. donegani* n. sp. HT male, Serranía de los Yariguíes, Colombia. **B.** *I. erebioides* Arcabuco, Boyacá, Colombia. **C.** *Tamania jacquelineae* PT, PNN El Tamá, Venezuelan side. **D.** *I. eremita* PNN El Tamá, Colombian side. Dorsal and ventral views on the right and left handsides respectively.

Habitat and ecology. Yariguíes páramo is characterised by low vegetation with spiny plants (Figs. 5A-B). We observed Blechnaceae ferns (*Blechnum schomburgkii*), Eriocaulaceae (*Paepalanthus*), Ericaceae, Clusiaceae, Bromeliaceae, Melastomataceae, Orchidaceae and Asteraceae (e.g. *Espeletia*) in this habitat. Other shrub species were present, with some isolated palms and dry shrubs of less than 1.5m height. Other *Idioneu-*

rula and *Tamania* species occur in marshy areas (bogs) and their host plants are grasses (e.g. *Calamagrostis*, *Stipa*) or sedges (Cyperaceae) (Pyrz 1995; Pyrcz & Vilorio 2007), whilst *I. donegani* was not found in marshy habitat. Few Gramineae and Cyperaceae plants were however found in *I. donegani*'s habitat below and at the treeline. In this habitat, there is frequently direct sunlight from about 0800hrs to midday, and then in the afternoon strong winds, torrential downpours and violent thunderstorms occurred daily. *Idioneurula donegani* was observed with greater frequency in Filo Pamplona, possibly due to the season of collection (end of rainy season). *I. donegani* was frequently seen on ground-dwelling plants of *Paepalanthus* (*Platycaulon*) Mart. (Eriocaulaceae) and flying no more than 1.5 m above ground level. It is active when ground-level mist or cloud is present and less active during times of strong insolation. When resting, it holds its wings in an unusual manner ($<180^\circ$) (multiple observations). It rests during the afternoon and during rain was observed under the leaves of an ericaceous plant (Fig. 5D).



FIGURE 3. Wing venation detail of *I. donegani* n. sp.

Etymology. The name *donegani* is formed as the genitive singular of a fictional second declension masculine Latin noun. The epithet is dedicated to Thomas Michael Donegan, EBA project director and a pioneer of the expeditions to Serranía de los Yariguíes. Fieldworker and researcher in Colombia for 10 years, Thomas has contributed to our knowledge of Colombian biodiversity through exploration, description of various new bird taxa and by supporting young Colombian researchers. Beloved husband and co-worker of the first author.

Conservation. In addition to *Idioneurula donegani*, the Serranía de los Yariguíes harbours a number of undescribed and recently described taxa (e.g. Donegan & Huertas 2006; Donegan *et al.* 2007; Huertas & Ríos MS). Despite topographical difficulties and complexity of access, human pressure for agriculture and livestock are mounting issues. During the EBA and YARÉ expeditions, deforestation, hunting and anti-personnel landmines were observed, complicating conservation efforts. Conservation of páramo habitats is clearly necessary for this species. In the YARÉ project, considerable conservation-oriented community work was carried out (see further in Huertas & Donegan 2006). Deforestation and other threats could potentially be reduced through education programmes and encouraging treatment of páramos as water sources that should not be modified. Subsequent to the EBA and YARÉ projects' fieldwork and other important local input, Serranía de los Yariguíes was declared a National Park (Ministerio del Medio Ambiente, Desarrollo y Vivienda 2005), an Alliance for Zero Extinction site (Ricketts *et al.* 2005) and an Important Bird Area (AICA) (Franco & Bravo 2005). Additionally, Fundación ProAves has established a nature reserve in the region.

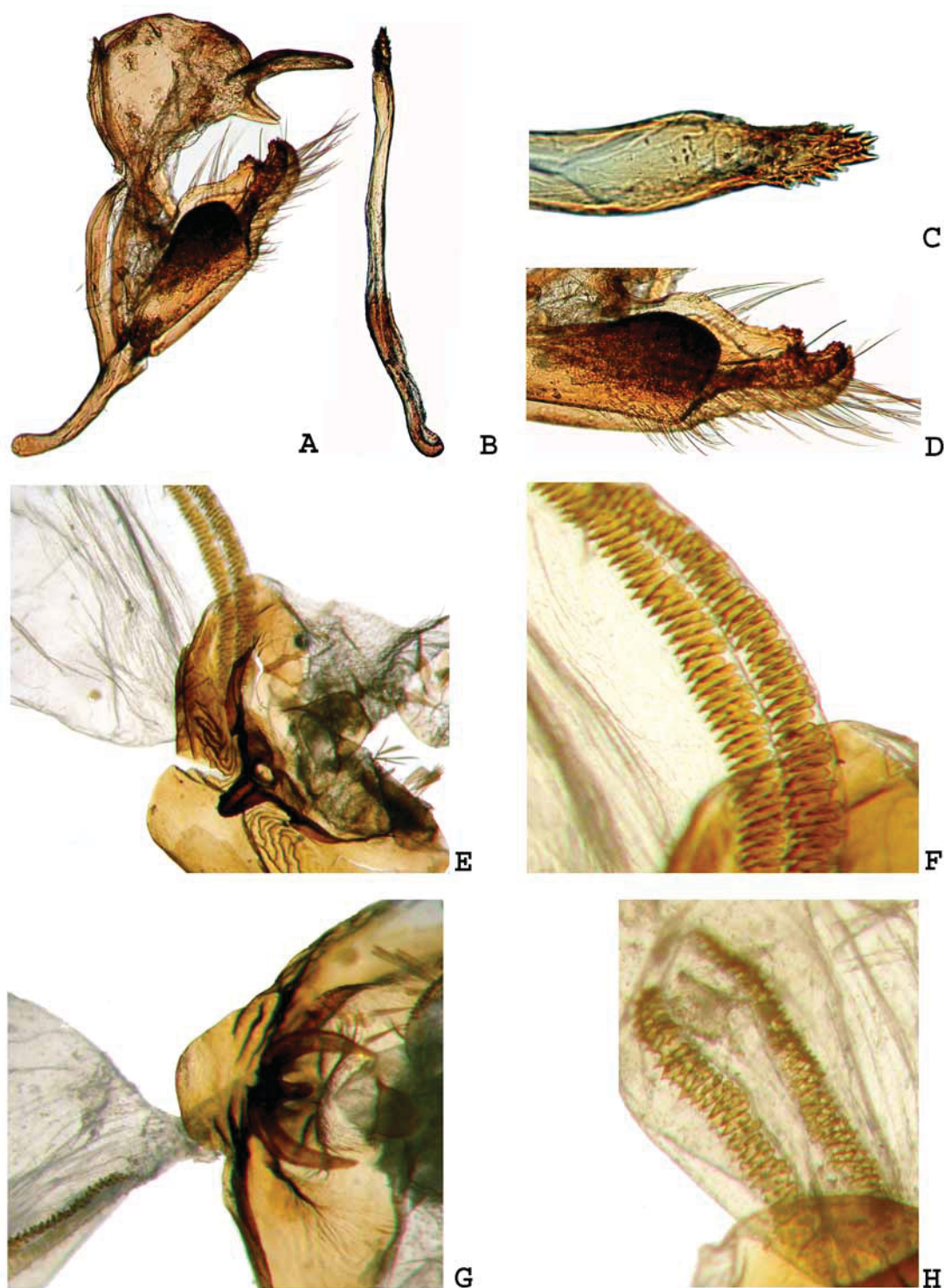


FIGURE 4. Figures A–D: *Idioneurula donegani* n. sp. A. Male genitalia B. Aedeagus C. Aedeagus detail D. Valvae detail E. Female genitalia, sterigma detail F. Signa detail. Figures G–H: *I. erebioides* G. Female genitalia, sterigma detail H. Signa detail.

A range and conservation assessment follows, based on the assumption that *I. donegani* is endemic to Serranía de los Yariguíes, considering the number of *Idioneurula* specimens inspected from nearby regions. The Yariguíes mountains attain suitable elevations for this species (over 3000m) with undisturbed habitat for c.25 km of their length and an average of c.1000 m laterally (IGAC 1995; IGAC 1999), producing an estimated area of suitable habitat of 25 km² for the new species. We have insufficient data to determine a population

estimate for *I. donegani* or population trends which are important for conservation assessments. However, the relative intactness and remoteness of habitats at high elevations in the Yariquíes suggests that the population is unlikely to be declining by >30% over ten years (IUCN criterion A), nor that the habitat is "severely fragmented" (IUCN criterion B). The inaccessibility of the new species' habitat, *I. donegani*'s relative abundance where found and the protected status of the Serranía de los Yariquíes each give some hope for the species' long term conservation. However, *I. donegani*'s apparently very small range mean that it should be categorised as a threatened species (Vulnerable) under category D2 (known from less than 5 localities).

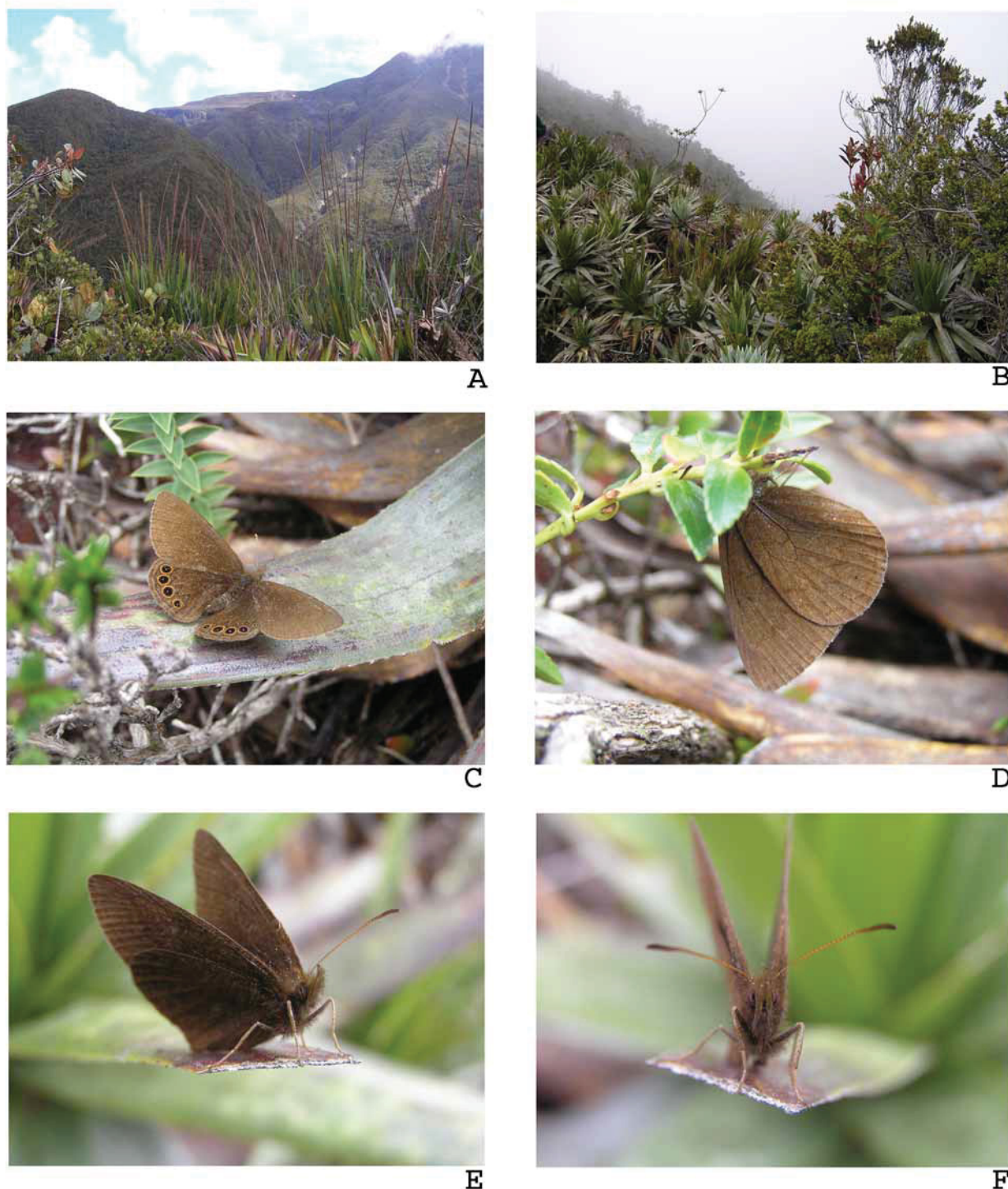


FIGURE 5. **A.** Serranía de los Yariquíes páramo type locality. **B.** Habitat where *Idioneurula donegani* n. sp. was collected. **C–D.** *I. donegani* n. sp. resting during daylight. **E–F.** *I. donegani* n. sp. head and leg detail.

Discussion

The number of species in the formerly monobasic genera *Idioneurula* and *Tamania* has doubled in 2007. Recently-described *I. eremita* and *I. donegani* are both distinctive in their morphology, suggesting that they had gone undescribed due to a lack of collecting efforts at high elevation sites of the Andes of eastern Colombia and western Venezuela.

We do not recognise either of the two described 'forms' of *I. erebioides* as valid taxa, even at subspecies level. The taxon *I. erebioides f. moderata* was described as having only one ocellus on the FW and more extensive white stripes in HW ventral (Weymer 1911) whilst *I. erebioides f. intermedia* purportedly has no HW dorsal white stripes but 2–3 ocelli in the HW (Apolinar 1914). We examined a large series of specimens (Appendix 1), noting presence or absence of white stripes on the HW ventral surface, and the number of ocelli on the dorsal and ventral HW and collecting locality. The number of dorsal HW ocelli varied in *I. erebioides* from 1 to 4; also in *T. jacquelineae* the number of dorsal HW ocelli varied from 3 to 4 and in *I. donegani* from 4 to 5. A sufficiently large series of *I. eremita* was not available to consider variation. Neither the number of ocelli present nor the presence or absence of white stripes on the HW in *I. erebioides* follows any biogeographic pattern. Stripes on the HW were not correlated with number of ocelli or sex. Further, no significant differences were found in male genitalia of individuals from different localities (n=5). These data indicate strongly that variations referred to in the descriptions of the two forms *moderata* (Weymer, 1911) and *intermedia* (Apolinar, 1914) are a product of individual, not geographical, variation, as suspected by Lamas & Vilorio (2004).

At the time it was described, *Tamania jacquelineae* was considered sufficiently different from *Idioneurula erebioides* to be placed in its own monobasic genus. We consider that, at the time, this was a reasonable approach. However, *I. donegani* and *I. eremita* are intermediate in certain characters between the two aforementioned taxa (such as in wing morphology and particularly genitalia), calling into question the validity of *Tamania*. Pyrcz (1995) noted that the ocelli pattern in *Tamania*, particularly the prominent M2-M3 cell ocelli on the dorsal and ventral surfaces, was "exclusive not only among the Pronophilini, but also, as it seems, among the Satyrinae worldwide". However, whilst FW ocelli were considered and remain a unique diagnostic feature of *Tamania*, patterns of presence and absence of FW ocelli occur among species in other related Satyrinae genera (e.g. *Lymanopoda* Westwood 1851, *Manerebia* Staudinger, 1897 and oriental *Ypthima* Hübn., 1818) and the number of ocelli on the dorsal HW varies considerably both among and within *Idioneurula* species. Although we do not seek to imply that, generally-speaking, ocelli are taxonomically uninformative, expression of ocelli should be relied upon with care in diagnosing butterfly genera.

Male genitalia morphology suggests that *I. erebioides*, *I. eremita*, *I. donegani* and *T. jacquelineae* are closely related. All of them show similar uncus and valva shapes, with the proximal opening for the aedeagus hirsute and concave and small spines on the proximal tip of the aedeagus. In *I. erebioides*, the valva are flatter and vinculum shorter. In *I. eremita*, the subuncus is smaller and closer to the uncus and the distal process of the valva is notably different than in other species. In *T. jacquelineae*, the tegumen is more pointed and the dorso-proximal valva is sclerotized (cf. disto-proximal in *I. donegani*) and more hirsute.

Female genitalia analysis of *I. erebioides* and *I. donegani* showed more conclusive variation between the species. In *I. erebioides*, the sterigma is elongated and more triangular, with conspicuous antler-like structure beneath the ostium bursae, with smaller bursa and shorter signa - about one half length of corpus bursae (Figs. 3G–H). The female genitalia of *Tamania* appear to be broadly similar to those of *I. donegani*, as far as one can tell from the description and the small and rather sketchy illustration (Pyrcz 1995). Analysis of female genitalia has been overlooked in many studies, possibly influenced by lack of available specimens, but has produced useful characters for analysis in recent studies of complex groups (e.g. Hall 1999, 2005; Willmott 2003). Such characters are worthy of further study in the Satyrinae.

I. eremita and *T. jacquelinae* were found to be more closely related to one another than other species studied in a recent study of Satyrinae (Peña *et al.* 2006). Preliminary results of molecular analysis including *I. donegani* show it to be c.3.5% different from *T. jacquelinae* and c.4% different from *I. eremita*, based on sequences reported by Peña *et al.* (2006). *T. jacquelinae* and *I. eremita* are c.2% different from one another. In the preliminary tree produced, *T. jacquelinae* and *I. eremita* were sister taxa, with *I. donegani* basal to them (Huertas & Lees unpubl. data). Levels of molecular divergence observed between *Tamania* and *Idioneurula* species are more typical of intrageneric than intergeneric molecular variation for this molecular marker in Satyrinae (Peña *et al.* 2006). This is a preliminary approach in light of the lack of molecular samples of *I. erebioides*.

Samples of species of genera found by Peña *et al.* (2006) to be more closely related than others to *Idioneurula*, such as *Lymanopoda* Westwood, 1851, *Ianussiusa* Pyrcz & Vilorio, 2004 and *Manerebia* Staudinger, 1897 are each >8% divergent from *I. donegani* (Huertas & Lees unpubl. data). *Diaphanos* Adams & Bernard, 1981 was not studied. Its relations with *Idioneurula* require further investigation.

Morphological and preliminary molecular results lead us to conclude that subdividing *Idioneurula* into two genera, as proposed by Pyrcz (1995) is no longer supportable. The characters of an expanded genus *Idioneurula* would be those set out in the diagnosis section above, with the exception of the former character “no markings on the dorsal forewing”, as *T. jacquelinae* has ocelli in this region. On the basis of apparent synapomorphies and the preliminary results of molecular analysis, we propose that *Tamania* Pyrcz, 1995 be regarded as a junior subjective synonym of *Idioneurula* Strand, 1932.

In conclusion, we propose recognition of the following species formerly classified as *Idioneurula* or *Tamania*, in the below linear order:

Idioneurula erebioides (C. Felder & R. Felder, 1867)

Idioneurula donegani n. sp Huertas & Arias, 2007

Idioneurula eremita Vilorio & Pyrcz, 2007

Idioneurula jacquelinae (Pyrcz, 1995)

Acknowledgements

Many thanks to J.C. Ríos for his help in the field, also to other YARE/EBA project team members: J. Aven-
daño, E. Briceño, T. Donegan, M. Donegan, J. Pinto, L. Rosado, D. Villanueva and D. Montealegre. Special
thanks to D. Lees (BMNH) for assistance in molecular analyses and valuable discussions; also to K. Sattler,
M. Honey and P. Ackery for their advice and help with genitalia analyses (BMNH). G. Martin (BMNH), J.
Clavijo (MIZA), J. Salazar (MHNUC), M. & C. Costa (MCPC), E. Castillo (IAvH), Hno. R. Casallas
(MHNUS), Efraín Henao (EHPC), T. Nguyen & M. Lagnel (MNHN) J. Hoogan (NHM-OU) provided access
to collections and J.F. Le Crom (JFLCPC) also thanks for *I. eremita* photo. K. Harman and team at Kew Gar-
dens, London identified various plants. Thanks to A. Vogler (BMNH) for providing laboratory facilities. Also
thanks to the communities of the municipalities visited. Corporación Autónoma Regional para la Defensa de
la Meseta de Bucaramanga (CDMB), Corporación Autónoma Regional de Santander (CAS), and the mayors
of San Vicente de Chucurí, Galán and El Carmen and sub-mayorality of Yarima provided the necessary per-
missions for field work (CAS Res no. 00832 of 2004). The EBA and YARÉ expeditions were supported by
the BP Conservation Programme (BirdLife International, Conservation International, Flora & Fauna Interna-
tional, Wildlife Conservation Society), Royal Geographical Society, Rio Tinto plc, Duke of Edinburgh, Fondo
para Acción Ambiental, Fundación Omacha, Conservation International Colombia (Becas Iniciativa de Espe-
cies Amenazadas—Jorge Ignacio “El Mono” Hernández-Camacho), the Percy Sladen Memorial Fund (Lin-
nean Society), Fundación ProAves, Game Conservancy Trust, World Pheasant Association, UIS, MHN-UC,
U. del Tolima, Gobernación de Santander and especially Huertas family. The authors acknowledge to the

Tropical Andean Butterfly Diversity Project (DEFRA, Darwin Initiative). Many thanks to A. Neild, T. Pyrcz and A. Viloría for their sharing data and valuable comments. We are in debt with K. Willmott and G. Lamas for their valuable comments and encouragement to publish this manuscript.

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Appendix 1. Material consulted

I. erebioides

64 males, 14 females

1 Male *Holotype* 'Bogotá', Uricoechea, L. *leg.*; 4 Males and 1 Female, 'Bogotá', Lindig Coll.; 2 Males & 1 Female, 'Bolivia'; 1 Male, Ven.; 1 Male, Nueva Grenada Río Magdalena a Bogotá, 1877, O. Thieme *leg.*; 1 Male 'Nueva Grenada'; 2 Males, Col., env. Bogotá, Apolinare Marie *leg.* de Bogotá; 8 Males & 1 Female, no data; 1 Male, Col., env. Bogotá, 1918, Apolinare Maria *leg.*; 2 Males and 2 Females Col., Las Hornas W below Arcabuco, dpto Boyacá, 2250m, 24-VII-1977, M.J Adams & G.I. Bernard *leg.*; 6 Males & 4 Females, Col., dpto Boyacá, W below Arcabuco, 2500m, 28-VII-1977, M.J Adams & G.I. Bernard *leg.*; 3 Males, Col., Sierra Nevada del Cocuy, border dptos. Boyacá & Casanare, above El Arenal, 2800–2850m, 2-VII-1977, M.J Adams & G.I. Bernard *leg.*; 3 Males, Col., SW El Arenal 2800–2850m, 2-VII-1977, M.J Adams & G.I. Bernard *leg.*; 4 Males, Col., dpto. Boyacá, SW above El Arenal (S of Lagunas Ocubí), S. Sierra Nevada el Cocuy, 2800–2850m, 11-VII-1977, Adams M.J. & G.I. Bernard *leg.*; 1 Male & 1 Female, Col., dpto. Boyacá, W slope of Colombian Eastern Cordillera, W 11 km below Arcabuco NE Side of Cañón, 2400m, 25-VII-1977, Adams M.J. & G.I. Bernard *leg.*; 1 Female, same data as previous, 2650m; 1 Female, Col., NE of El Arenal, 2500m, dpto. Boyacá, 15-VI-1977, Adams M.J. & G.I. Bernard *leg.* (all, BMNH). 5 Males, Col., dpto. Boyacá, Santuario de Fauna y Flora (SFF) Iguaque, between San Pedro de Iguaque and Villa de Leyva, 10:50 a.m. on 21-X-2005, E. Henao *leg.* (EHPC). 6 Males: Col., dpto. Santander, Veléz, road to Cimitarra, 2500m, 20-VII-1963, E. Schmidt M. *leg.* (SM4771/IAvH 8627); Col., dpto. Boyacá, Pajarito, Laguna de Tota, 2700m, 02-I-1983, E. Schmidt M. *leg.* (SM 4769/IAvH 8625); Col., dpto. Boyacá, Duitama, road to Charalá, 2700m, 02-I-1983, E. Schmidt M. *leg.* (SM 4770/IAvH 8626); Col., dpto. Santander, Charalá, 2900m, 11-X-1973, E. Schmidt M. *leg.* (SM 4772/IAvH 8628); Col., dpto. Cundinamarca, Subachoque, El Rosal-El Tablazo, 11-XI-1947, 3200m, E. Schmidt M. *leg.* (SM 4773/IAvH 8629); Col., dpto. Cundinamarca, Sumapáz, Páramo de Sumapáz, 3000m, 01-II-1980, E. Schmidt M. *leg.* (SM 4774/IAvH 8629) (all, IAvH). 3 Males: Col., dpto. Cundinamarca, Guasca, 26-III-1989, J.F. Le Crom *leg.*; Col., dpto. Cundinamarca, Facativá, 2900m, 7-I-1989, J.F. Le Crom *leg.*; dpto. Cundinamarca, Chía, 25-XII-1989, J.F. Le Crom *leg.* (all, JFLPC). 2 Males, Col., 'Bogotá', 1862, Sindig, M. *leg.*; 2 Males & 1 Female 'Col.', 1842, A. Parduzaki *leg.*; 2 Males, Col., Ur. Lindig *leg.* (probably PT); 1 Male, Col., Bogotá, 1862, Lindig *leg.*; 1 Male, Col., Bogotá, 2700m, 1910, A. H. Fassl *leg.*; 1 Male Col., Bogotá, 2700m, III-1910, A. H. Fassl *leg.* (all, MNHN). 3 Males, Col., dpto. Cundinamarca, Guasca, 26-III-1989, J.F. Le Crom *leg.*; Col., dpto. Cundinamarca, Facativá, 2900m, 7-I-1989, J.F. Le Crom *leg.*; Col., dpto. Cundinamarca, Chía, 25-XII-1989, J.F. Le Crom *leg.*; 1 Male, Col. (NHM-OU). Unsexed individual, Col., dpto. Cundinamarca, Páramo de Choachí, Hno. E. José, 29-XII-1913, 2800–3200m (record from literature: Apolinar, 1914).

I. eremita

2 Males

2 Males including 1 *Paratype*, Col., dpto. Norte de Santander, Parque Nacional Natural (PNN) El Tamá, 3200m, 22-XII-1993, J.F. Le Crom *leg.* (JFLCPC)

T. jacquelineae

6 Males; 1 Female

1 Male, *Type* Ven., edo. Táchira, PNN El Tama, Betania, 2500m, VIII-1977, T. Pyrcz *leg.*; 1 Female, *Paratype*, Ven. edo. Táchira, Betania, 19-IX-1987, T. Pyrcz *leg.* (both, MIZA). 2 Males, *Paratypes* 'Bolivia' (BMNH). 2 Males, Ven., Villa Páez, 2200m, 29-XII-1993, Costa & Costa, *leg.* (MCPC). 1 Male, Col., dpto. Santander, C. Chichira, X-1993, J. Valencia *leg.* (JFLCPC). 2 Males, Ven., edo. Táchira, PNN El Tamá, bosque arriba de Betania, 2400m, 15-VIII-1996, A. Viloria, V. Carrizo, D. & J. González *leg.*

I. donegani

See Holotype, Allotype and Paratypes data above.